

Research Article

Bottom-up control of whitefish populations in ultra-oligotrophic Lake Brienz

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Abstract. Lake Brienz, an oligotrophic pre-alpine Swiss lake, went through a mesotrophic period between around 1960 and 1990. The lake is moderately turbid caused by fine suspended solids from glaciers. In 1999, yield of the economically important whitefish collapsed to about 10 % of preceding years. Age and growth analysis of the two whitefish types examined – small and large type – revealed an almost complete halt of growth from 1999 until June 2000, paralleled by poor condition. Zooplankton data showed that cladocerans, the preferred food of whitefish, were rare from January 1999 until June 2000. In order to elucidate the trophic relationships between zooplankton and fish, the «Wisconsin Bioenergetics Model 3.0» was applied. The analysis showed that poor growth and condition of whitefish in 1999 and

2000 were caused by the scarcity of primary food organisms. The relatively small and slender fish could not be caught by legal gillnets, which resulted in poor fishing yield. Evidence is presented that cladoceran biomass governs food consumption by the fish («bottom-up effect»), while the effect of fish predation on cladocerans was found to be negligible, most likely also during the period of poor growth. Turbidity did not appear to significantly interfere with the feeding of whitefish. Growth, condition and commercial yield of whitefish partly increased again after 2000, but due to the very low productivity of Lake Brienz, fishing yield will remain low. Food chains in such oligotrophic systems are fragile. It is likely that a future collapse of the cladoceran population and, thus, the whitefish fishery will happen again.

Key words. Coregonids; fishing yield; food chain; bottom-up effects; bioenergetics model; oligotrophication.

Introduction

The production of fish biomass in natural waters is governed by primary production of the system, controlling zooplankton production, and mediated by the

size and composition of the fish community. In lakes, the relationship between lake trophic state (in terms of phosphorus concentration), primary production and fish production is well established (Gerking, 1978; Downing et al., 1990; Downing and Plante, 1993; Kaiser et al., 1994). In general, eutrophic lakes support much higher fish production and fishing yield than oligotrophic lakes. Conversely, decreasing trophic state, a process referred to as oligotrophica-

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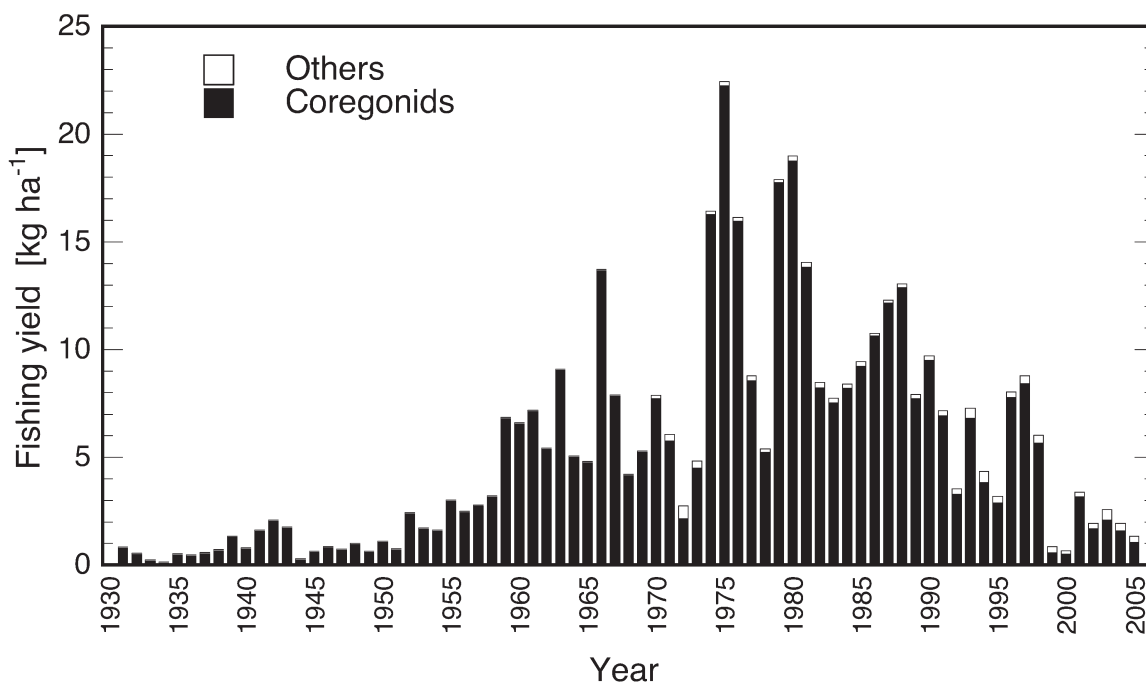


Figure 1. Fishing yield of the commercial fishery in Lake Brienz, years 1931–2005. Data obtained from the Fisheries Agency of the Canton Bern.

tion, leads to lower fish production and yield (Müller and Mbwenemo Bia, 1998; Eckmann and Rösch, 1998). While a decrease in total phosphorus concentration from very high ($>150 \mu\text{g L}^{-1}$) to moderately high values ($30\text{--}60 \mu\text{g L}^{-1}$) has rarely caused a significant drop in fishing yield (Müller and Stadelmann, 2004), fish production and yield tend to decrease quite rapidly at the lower end of the phosphorus scale, i.e. below $10\text{--}15 \mu\text{g L}^{-1}$ (Jeppesen et al., 2005; Rellstab et al., 2004). Thus, primary production seems to effect the food chain more profoundly at low nutrient levels. Furthermore, the interaction between fish as predators and zooplankton as prey complicates the situation in the course of oligotrophication, because zooplanktivorous fish may eliminate large grazers such as daphnids (Gaedke, 1999; Stich et al., 2005). Daphnids could eventually be replaced by smaller and less efficient grazers. This would further reduce fish production to a value well below the level expected based on primary production.

The major lakes of the Alpine region are typically deep, cold and oligotrophic. This was true until the onset of cultural eutrophication in the first half of the 20th century. Between about 1960 and 1990, Swiss lakes passed through a temporary mesotrophic or even eutrophic phase. Some lakes have remained eutrophic (Liechti, 1994).

Two forms of European whitefish (coregonids) have dominated the fish fauna of Lake Brienz as

reflected in the fisheries statistics (Fig. 1): the slow-growing “Brienzig” (hereafter referred to as “small type”), *Coregonus albellus* Fatio, and the fast-growing “Felchen” (hereafter referred to as “large type”), *C. fatioides* Kottelat (nomenclature according to Kottelat, 1997). Even though there are one or two more forms present in the lake (Kirchhofer, 1990; Bernatchez and Dodson, 1994; Douglas, 1998), these are not easily identifiable and at present not numerically important for the fishery. Fishing yield during the mesotrophic phase in 1970–1990 averaged 10.9 kg ha^{-1} with a whitefish fraction of 98%. In 1999 whitefish yield collapsed to 0.6 kg ha^{-1} from 8.4 kg ha^{-1} in 1997 and 5.7 kg ha^{-1} in 1998 (Fig. 1). Yield was still low in 2000 but reached somewhat higher values in the following years. The collapse of the fishery prompted the authorities of the Canton Bern to initiate a comprehensive research project aimed at identifying the causes of the collapse, including all major factors acting on the ecosystem of Lake Brienz (Wüest and Zeh, 2007). Special attention was given to mechanisms underlying the collapse of the fishery and to the question if and how future collapses could be prevented.

In this work, major population parameters of the two most important whitefishes in Lake Brienz, such as growth, condition and year class strength, are presented. These data, together with data on zooplankton abundance in the lake, are then incorporated into a bioenergetics model for exploring the cause of

the catch decline. Special attention was given to daphnids, the main food category in many whitefish populations (Rufli, 1979; Becker and Eckmann, 1992; Mookerji et al., 1998). Furthermore, a model of zooplankton–fish encounter probabilities was used to study the effect of food density and visibility on fish feeding and growth. The results of these models should help to formulate a prediction about future yield of the whitefish fishery in Lake Brienz, one of the main questions of the overall research project. The objective of this work was to test three hypotheses: 1. Zooplankton concentration in 1999 and 2000 was the driving force behind the catch decline (“bottom-up effect”); 2. The whitefish population exerted top-down control of the zooplankton population in Lake Brienz during 1995–2003; and 3. Elevated turbidity had a strong negative effect on the feeding of the whitefish in 1999 and 2000. These hypotheses are tested at the level of populations (H1 and H2) and individuals (H2 and H3).

Materials and methods

Lake Brienz, the uppermost large natural lake in the River Rhine catchment in Switzerland, reached a maximum of about $20 \mu\text{g L}^{-1}$ total phosphorus (TP) during 1980–1984. By the year 2000, TP and soluble reactive phosphorus (SRP) had decreased to about 7 and $1 \mu\text{g L}^{-1}$, respectively, due to effective water protection measures (Müller et al., 2007). Today, most TP is in a biologically inactive mineral form. The lake (surface area 29.8 km^2 , maximum depth 260 m) receives considerable amounts of finely divided solids from glaciers that affect visibility and light penetration in the lake (Jaun et al., 2007). Data on primary production are scarce and can, for most of the time considered here, only be inferred from SRP values (Müller et al., 2007). In 1987 primary production was $100 \text{ g C m}^{-2} \text{ a}^{-1}$ (Kirchhofer, 1990), whereas in 2004 it was $66 \text{ g C m}^{-2} \text{ a}^{-1}$ (Finger et al., 2007). Maximum biomass of daphnids and total zooplankton decreased from $32.7\text{--}38.6$ and $47.4\text{--}50.2 \text{ g m}^{-2}$ wet weight (range) in 1995–1996 to $6.8\text{--}16.7$ and $23.6\text{--}26.6 \text{ g m}^{-2}$ in 2001–2004, respectively. For detailed characteristics of Lake Brienz see Wüest and Zeh (2007).

Data and scale samples of Lake Brienz whitefish were obtained from the Fisheries Agency of the Canton Bern. The agency has been conducting a monitoring programme since 1984 by monthly sampling 25 whitefish from commercial gillnet catches (Kirchhofer, 1995; Kirchhofer et al., 2005). The fish sampled are measured and weighed, sexed, gillrakers counted for species identification, and scale samples taken for age and growth determination. The prime

objective of the monitoring programme is to properly manage the whitefish populations, particularly for setting the legal mesh size of gillnets. Bar mesh size of the gillnets used in the commercial fishery until 1992 was 35–40 mm for bottom set nets used in winter, and 38 mm for floating nets used in spring, summer and autumn. In 1993, to counteract decreasing yields due to slower growth of whitefish, the legal mesh size was lowered to 30 mm for bottom set nets and to 35 mm for floating nets. From 1996, the legal mesh size of floating gillnets was 30 mm (Table 1). In 2004, small type whitefish were specifically caught with 20 mm nets on an experimental basis only.

The data used for this study comprised 5909 fish from years 1984–2004, including 347 fish from special catches in 1999, 2000 and 2001 with small-meshed nets (10–20 mm bar mesh). Scale age readings of all fish were verified, and a sub-sample of 1790 scales (49–364 per year) was measured for growth calculations. Growth was back-calculated using a binomial regression of total scale radius versus total length. Because back-calculated lengths showed bimodal length distributions at age 2 and older, all fish were assigned to either small type or large type whitefish by applying a cohort-specific threshold value for length-at-age (Müller, 2003). Condition was expressed by Fulton’s condition factor $K [-]$ as

$$K = W 10^5 L^{-3} \text{ where } W = \text{fish weight [g]} \\ L = \text{total length [mm]}.$$

Table 1. Size and composition by type of whitefish catch samples from the monitoring programme, years 1984–2004, and sampling mesh size (bar length). Only samples from nets of legal mesh size, with the exception of 2004 when small-type whitefish were specifically sampled with 20 mm nets.

Year	Sample size (no. of individuals)	Large type %	Small type %	Mesh size (mm)
1984	267	92.5	7.5	35, 38, 40
1985	272	79.0	21.0	35, 38, 40
1986	274	24.5	75.5	35, 38, 40
1987	275	26.5	73.5	35, 38, 40
1988	262	24.4	75.6	35, 38
1989	274	31.8	68.2	35, 38
1990	275	59.3	40.7	35, 38
1991	275	54.5	45.5	35, 38, 40
1992	260	50.4	49.6	35, 38
1993	275	60.7	39.3	30, 35, 38
1994	275	59.3	40.7	30, 35, 38
1995	264	53.4	46.6	30, 35
1996	275	81.5	18.5	30, 38
1997	275	48.4	51.6	30, 35, 38
1998	274	54.7	45.3	30, 35, 38
1999	155	46.5	53.5	30, 40
2000	140	84.3	15.7	30
2001	274	100.0	0.0	30
2002	263	97.3	2.7	30
2003	200	98.0	2.0	30
2004	275	49.8	50.2	20, 30

The size of individual year classes was calculated in a worksheet application by virtual population analysis VPA (Ricker, 1975; Megrey, 1989; Haddon, 2001) and by adding an annual 20% natural mortality rate (Eckmann et al., 2002) for age classes two to eight. For calculating cohort size, the weight of the annual catch was assigned to small and large type whitefish according to the proportion and the mean weight in the monitoring samples. Changes in catch intensity were not included.

Trophic relationships between whitefish and zooplankton were assessed using the «Wisconsin Bioenergetics Model 3.0» (Hanson et al., 1997). This model is based on an energy balance equation, including consumption, total metabolism, waste losses and growth:

Consumption C = (respiration + active metabolism + specific dynamic action) + (egestion + excretion) + (somatic growth + gonad production).

Using observed values of population structure and estimated population size from VPA and individual growth per year and year class for small type and large type whitefish separately, the model calculates the amount of energy consumed by the fish on a daily basis as specific consumption rates in $J\ g^{-1}$ of fish. Energy is then converted into biomass of food organisms consumed, i.e. zooplankton here. Estimates of physiological parameters for whitefish metabolism (weight-dependent values for swimming speed, respiration, egestion and excretion) were taken from the «generalized coregonid model» by Rudstam et al. (1994; cit. in Hanson et al., 1997) in accordance with the procedure by Eckmann et al. (2002).

Consumption C [$g\ g^{-1}\ d^{-1}$] was adjusted to the annual variation in water temperature and to fish weight by

$$C = C_{\max} p f(T) \text{ where}$$

C_{\max} = maximum consumption rate, p = scaling factor [-] of C_{\max} ($0 < p < 1$) accounting for ecological constraints on the maximum feeding rate, $f(T)$ = temperature dependence function [-] describing weight dependence at optimum and maximum temperature values, and

$$C_{\max} = CA W^{CB} \text{ where}$$

W = fish weight [g], CA and CB = parameters of weight dependence function at optimum water temperature (Hanson et al., 1997).

The scaling factor p is calculated to adjust the estimated growth based on physiological parameters

to the observed growth for each year class and year of study; p varied between 0.15 and 0.34 for large type whitefish and between 0.12 and 0.22 for small type whitefish. Water temperatures were taken from the 0–30 m depth range in temperature profiles measured monthly by the Laboratory for Water and Soil Protection of the Canton Bern (GBL) from 1994–2004, and $f(T)$ is then calculated with temperature dependence values for warm-water species from Kitchell et al. (1977; cited in Hanson et al., 1997). Energy content of whitefish ($13,060\ J\ g^{-1}$), daphnids and copepods ($2513\ J\ g^{-1}$), and *Bythotrephes* and *Leptodora* ($949\ J\ g^{-1}$) were taken from Eckmann et al. (2002). Detailed stomach data for Lake Brienz whitefish (large type only) were from Maurer and Guthruff (2005). Energy losses due to reproduction were not included in the model.

The following population parameters were used in the bioenergetics model: cohort size at the start of the year, estimated fishing mortality according to catch statistics per month (only commercial catch), estimated average natural mortality per day, and mean individual weight of cohorts at the start and the end of the year. Specific consumption rates by small type and large type whitefish were first calculated as g of zooplankton per g of fish d^{-1} . These were then integrated to determine the total weight of zooplankton consumed by the whitefish population per day and summed to consumption per year. Growth, condition and consumption were compared with integrated zooplankton composition and biomass over the whole lake (data from Rellstab et al., 2007) to test hypothesis 1 about the «bottom-up effect» of catch decline. In periods with no daphnids in zooplankton samples, a density of $43\ Daphnia\ m^{-2}$ (i.e. just below the detection level according to Rellstab et al., 2007) was assumed. Furthermore, *Daphnia* standing crop was related to total consumption by the whitefish population with a linear regression analysis in order to test hypothesis 2 about «top-down control» of the *Daphnia* population. A positive correlation between *Daphnia* standing crop and total daphnid consumption by the whitefish population would indicate a «bottom-up effect», whereas a negative correlation would indicate a «top-down effect».

Whitefish forage by vision and by snatching individual food items while cruising the lake. Therefore, *Daphnia* can only serve as food to whitefish if they are seen and if they are available in sufficiently high densities. To study these relations between *Daphnia* and individual whitefish, encounter probabilities were calculated by applying the model of visual range in fish by Aksnes and Giske (1993) and Aksnes and Utne (1997). Maximum encounter rate E in terms of daphnids s^{-1} was calculated as

$$E = \pi (r \sin \Theta)^2 v N \text{ [s}^{-1}\text{]}$$

where $r \sin \Theta$ = «funnel searched» with r = radius [m] and Θ = half angle of vision inside which the prey is seen and attacked, v = swimming speed [m s^{-1}], N = prey density (adult daphnids only) [m^{-3}].

The resulting maximum consumption rate f [s^{-1}], which gives the number of prey s^{-1} and allows for handling time h [s] for capture and swallowing, is

$$f = \frac{h^{-1}N}{(h\pi(r \sin \Theta)^2 v)^{-1} + N} \text{ [s}^{-1}\text{]} \quad (1)$$

We used the following parameters:

$r = 0.05$ and 0.1 m for 1–2 mm size *Daphnia* (Link, 1996; Vinyard and O'Brien, 1976).

$\Theta = 112.5^\circ$, as found in the laboratory for *Coregonus artedii* (Link, 1996, 1998).

$v = 0.3 \text{ m s}^{-1}$, corresponding to an average cruising speed of 1–2 body lengths s^{-1} for large type and small type whitefish, which seems realistic as Jobling (1995) postulates 1–3 body lengths as usual optimum swimming speed, and Büttiker (1975) estimated the cruising speed of whitefish in Lake Thun at 0.21 – 0.41 m s^{-1} by echo-sounding.

$h = 1$ s for handling and swallowing 1 *Daphnia* (Mittelbach, 1981),

N = observed adult *Daphnia* density [m^{-3}] (Rellstab et al., 2007).

The effect of increased turbidity on the feeding of whitefish was investigated by assuming that the «visual range» R [m] of the fish is shortened by reduced light transmission and light intensity, thus reducing the activity radius r (= «funnel searched») and finally the feeding rate f . The visual range R related to a target object can be expressed as a function of light, depth, target characteristics and an eye-inherent parameter (Aksnes and Giske, 1993; Aksnes and Utne, 1997):

$$R^2 e^{(cR+Kz)} = \rho E_0 |C_0| \pi \beta^2 \Delta S_e^{-1} \text{ [m}^2\text{]} \quad (2)$$

- c = beam attenuation coefficient [m^{-1}],
- K = vertical attenuation coefficient [m^{-1}],
- z = depth [m],
- ρ = irradiance loss at air-water surface (0.5 according to Aksnes and Giske, 1993),
- E_0 = irradiance at water surface [$\mu\text{E m}^{-2} \text{s}^{-1}$],
- C_0 = inherent contrast of target (0.5 according to Aksnes and Giske, 1993); changes in contrast due to changing turbidity were not considered,
- β = target radius (0.002 m),

ΔS_e = sensitivity threshold of eye for detection of changes in irradiance ($1 \times 10^{-7} \mu\text{E m}^{-2} \text{s}^{-1}$ according to Aksnes and Giske, 1993).

R has to be solved by iteration. At large depths, however, where $cR < 0.02$ ($cR + Kz$), cR can be neglected and R can be solved as follows (Aksnes and Giske, 1993):

$$R = (\rho E_0 \exp(-Kz) |C_0| \pi \beta^2 \Delta S_e^{-1})^{1/2} \text{ [m]} \quad (3)$$

The relation between visual range R , radius r of the funnel searched and encounter rate E of fish with *Daphnia* can be expressed such that E is a function of r when $R > r$, and E is a function of R when $R < r$. With these relationships, the effect of increased turbidity on the feeding rate of whitefish can be modelled under various conditions. Light intensity, transmission values and attenuation coefficients at depths 0–50 m in Lake Brienz from *in situ* measurements between January 1999 and December 2004 according to Jaun et al. (2007) were used to assess the effects of changes in light distribution on whitefish feeding and to test hypothesis 3. In addition, simulations of vertical distribution of suspended particles in the lake with and without upstream dams (Finger et al., 2006) were used to study the influence of hydropower on whitefish feeding as suspected by fishermen.

In order to assess sustainable fishing yield at actual food concentrations, the carrying capacity for the whitefish population of the whole lake was estimated assuming that 1.5 % of the standing crop of adult *Daphnia* is consumed per day. Rellstab et al. (2007) found that the mean net growth rate (which already includes a mean predation rate) of the *Daphnia* population varied between 1.5 and 9.4 % in spring 1986–2005. We therefore assume that the *Daphnia* population is not endangered as long as consumption by whitefish remains below 1.5 % of the standing crop per day. Carrying capacity is then compared to total consumption resulting from specific consumption rates as calculated with the bioenergetics model, and from feeding rates as calculated with the encounter model.

Results

The two coregonids made up highly varying proportions in the commercial catch, with large type whitefish contributing between 24.4 % and 100 % each year (Table 1). The share of large type coregonids in the samples from the special catches with small-meshed nets was 58.5 % in 1999 ($n = 41$), 34.6 % in 2000 ($n = 197$) and 9.0 % in 2001 ($n = 100$). In spite of the substantial reduction in legal mesh size between 1984

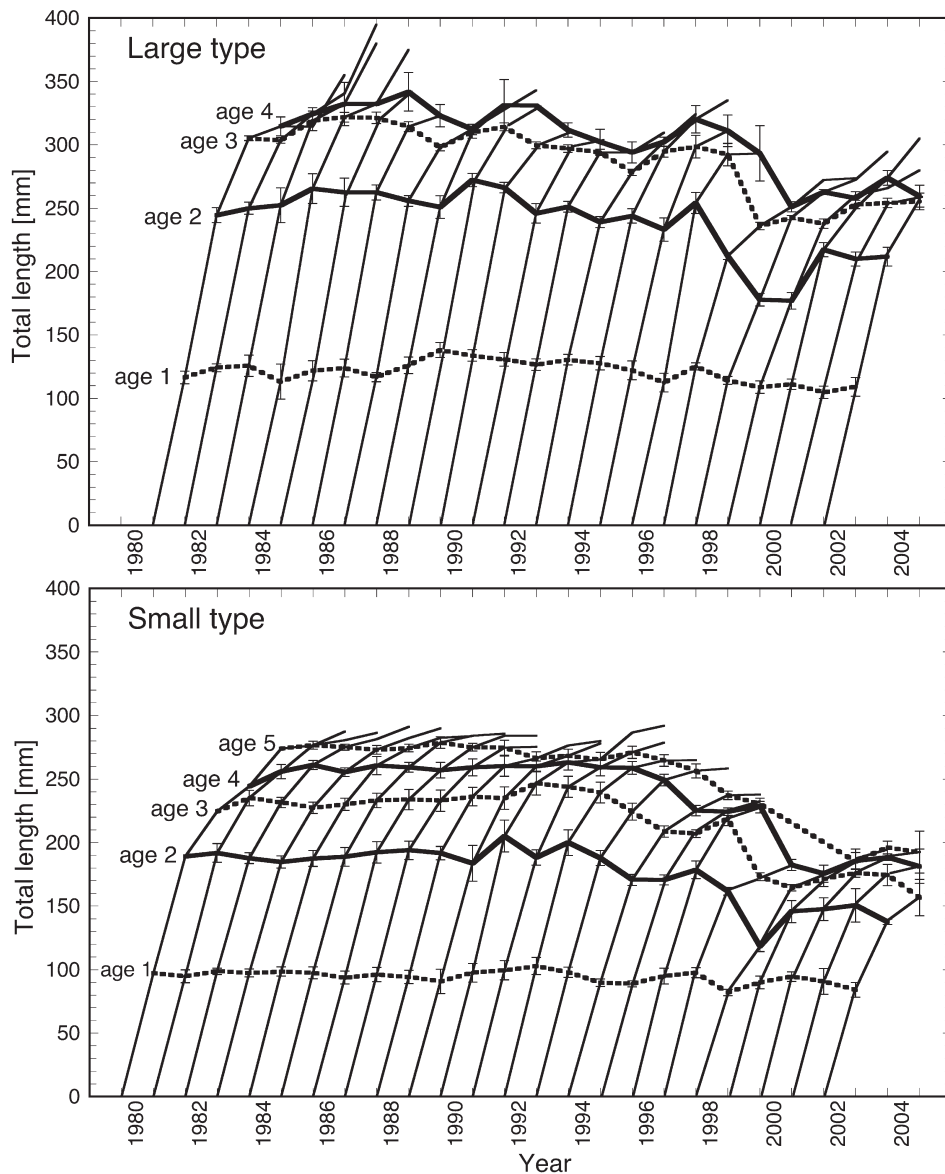


Figure 2 Growth of Lake Brienz coregonids, by cohort and age group. Top: Large type whitefish “Felchen” ($n = 2294$), bottom: Small type whitefish “Brienlig” ($n = 1675$). Error bars indicate 95 % confidence interval of the mean.

and 2004 (Table 1), average age-at-capture of large type whitefish increased from 2.61 years ($SD = 0.50$, $n = 247$) in 1984 to 3.16 years ($SD = 0.90$, $n = 137$; $t = 6.547$, $P < 0.001$) in 2004. Likewise, mean age-at-capture of small type whitefish in the legal-size gillnets increased from 3.17 years ($SD = 1.54$, $n = 18$) in 1984 to 3.93 years ($SD = 1.00$, $n = 89$; $t = 1.963$, n.s.) in 2004.

Growth in length of both types of coregonids was fair until the early 1990 s (Fig. 2). In the course of the 1990 s, growth slowly decreased. In 1999 and 2000, growth of both types strongly decreased in fish older than one year. After 2000, growth increased again but did not attain former values. In large type whitefish, length of year classes 2000–2002 at age 3 was 87 % of

that of year classes 1990–1995. In small type whitefish, however, growth remained poor with fish barely reaching 20 cm in length even at age 5, as compared to 27–28 cm before 1995.

Growth of Lake Brienz whitefish in terms of annual length increments was compared with the abundance of adult daphnids. There was a significant positive linear relationship between growth of small type whitefish and daphnid biomass in Lake Brienz during the main growing season from May to September, with the exception of fish in their first year. For large type whitefish, the relationship was also positive but not significant, with the exception of fish in their fourth year (Fig. 3, Table 2). Also, data for

Table 2. Regression parameters of Figure 3: $dL/dt = a + b B$. P indicates significance of the slope b.

Growth type	a [mm]	b [mm]	r ²	n	P
Large year 1	108.7	0.940	0.22	8	0.24
Large year 2	79.9	4.264	0.35	9	0.09
Large year 3	41.8	1.156	0.08	10	0.43
Large year 4	7.9	1.848	0.55	9	0.02
Small year 1	88.1	0.436	0.08	8	0.50
Small year 2	42.8	4.291	0.81	9	0.001
Small year 3	21.4	2.058	0.40	10	0.049
Small year 4	7.6	1.482	0.84	10	0.0002

large type whitefish showed more variation than data for small type whitefish.

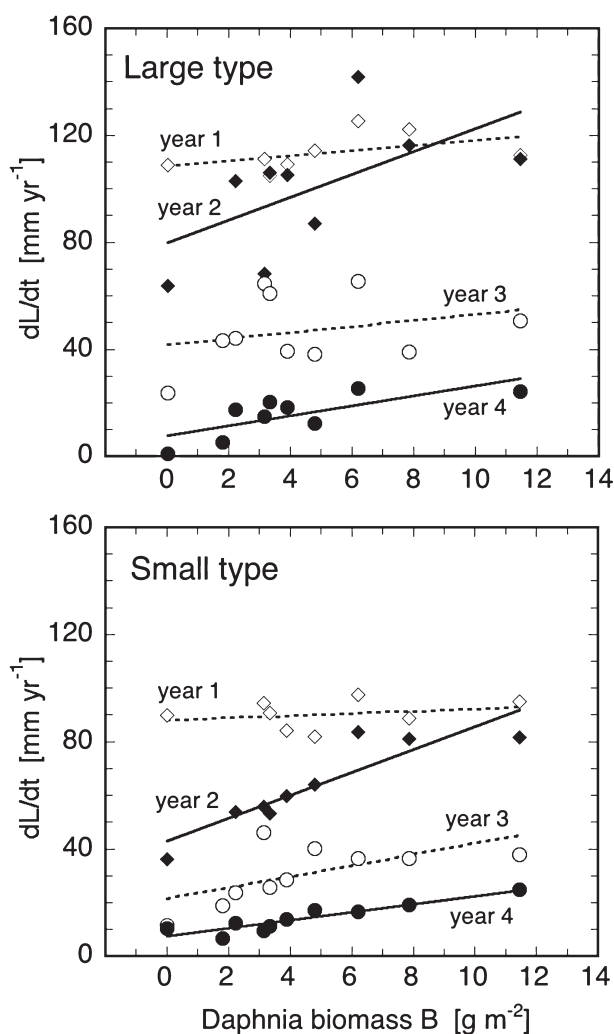


Figure 3. Relationship between mean adult *Daphnia* biomass B in Lake Brienz, May to September 1995–2004, and mean annual length increase dL/dt in large type and small type whitefish, year classes 1993–2002 (from Figure 2). For regression parameters see Table 2.

In parallel with growth, condition slowly decreased during the 1990 s (Fig. 4). As in growth, condition

reached the lowest values in 1999 and 2000. Condition of small type whitefish was significantly lower than that of large type whitefish in years 1990–1996, 1999–2001 and 2003–2004. In both types, mean condition values in 1999 and 2000 were significantly lower than during the four years before 1999 and after 2000 (two-tailed t-tests, $P < 0.01$). While condition of large type whitefish after 2000 regained values observed before 1995, condition of small type whitefish did not fully recover after 2000.

Cohort size by number of large type whitefish, as calculated by VPA, varied according to year class but did not exhibit any clear trend (Fig. 5). Conversely, cohort size by number and biomass of small type whitefish strongly decreased, starting already with the cohort in 1984. Combined biomass of both types of coregonids decreased from some 220 tons for cohort 1982 to about 8 tons for cohort 1996 and 11 tons for cohort 1999. It should be noted here that the size of small type cohorts 1997 and later most likely was grossly underestimated because this coregonid could not be caught effectively in the commercial nets due to its small size.

Consumption of daphnids by the whitefish population, as calculated with the bioenergetics model and assuming exclusively adult *Daphnia* as food organisms, followed the general evolution of trophic state and *Daphnia* abundance of Lake Brienz (Fig. 6). Maximum consumption was between 2600 and 3800 kg d⁻¹ in 1994–1996 but decreased to less than 1000 kg d⁻¹ in 1998 and later. The lowest value was found in 1999 when the daphnid population was almost absent. Until 1998 consumption by both types of whitefish showed a similar annual cycle. However, from 1999 on, consumption by small type whitefish apparently did not recover. This is considered an artefact due to the underrepresentation of this whitefish type in the monitoring samples (see above). According to Madenjian et al. (2006), consumption estimates of whitefish, based on physiological parameters of the «generalized coregonid model» (Hanson et al. 1997), might be substantially overestimated. Comparing mean weight of individuals estimated with the bioenergetics model to observed individual mean

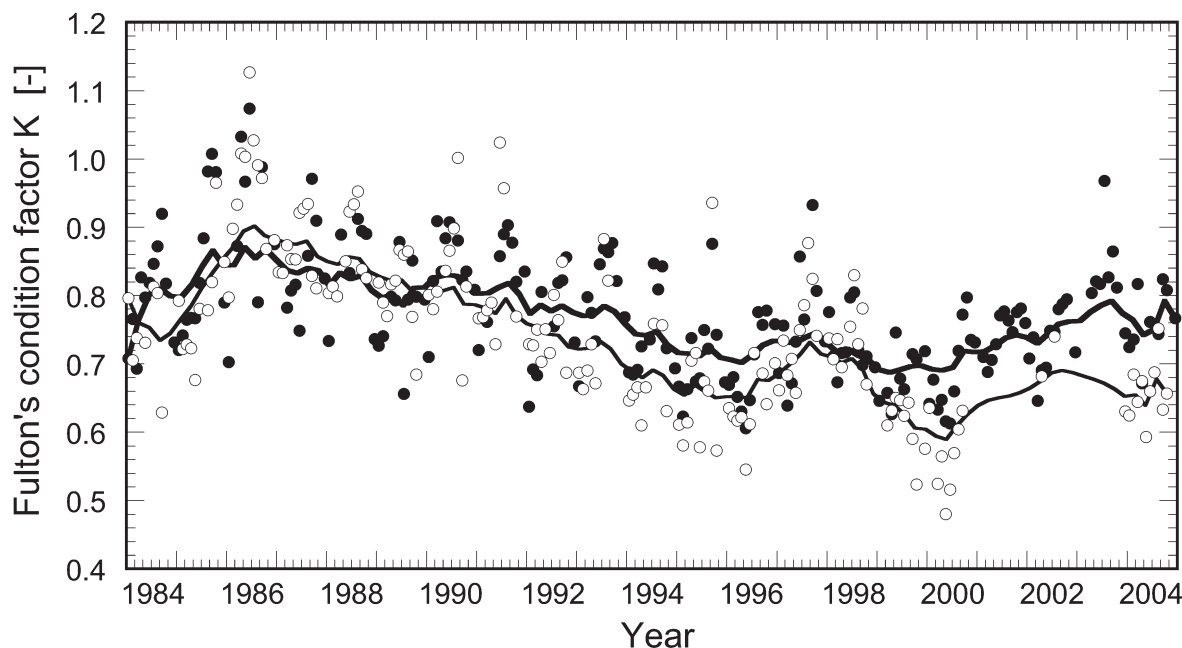


Figure 4. Fulton's condition factor K for large type (dark points, thick line) and small type coregonids (light points, thin line), based on monthly averages for each type. A smooth curve was fitted to these points for each coregonid using locally weighted least-squares (Stineman function in software KaleidaGraph V3.6 by Synergy Software).

weight from monitoring data by month also shows that calculated weight from the bioenergetics model is overestimated for fish below 150 g and underestimated for larger fish (linear regression with all year classes of large type whitefish and months studied: $W_{\text{estimated}} = 61.451 + 0.591 W_{\text{observed}}$, $r^2 = 0.536$). To account for this, consumed daily food rations were reduced by one third in further calculations.

Applying the encounter model to the observed *Daphnia* densities in the lake, the feeding rate of whitefish varied between <0.02 and $0.92 \text{ Daphnia s}^{-1}$ in 1994–2004, with minimum values far below $0.02 \text{ Daphnia s}^{-1}$ in 1999 and 2000. Daily food rations estimated with the bioenergetics model (as numbers of *Daphnia* d^{-1}), combined with the time needed to consume this ration according to the encounter model, at a day length of 8 (November–February), 12 (March–April and September–October) and 16 hours (May–August), reveals that the whitefish did not have enough time to consume their daily ration (Fig. 7). With concentrations at between 30 and 200 adult *Daphnia* m^{-3} , large type whitefish sometimes ran out of time, and with prey densities below 10 *Daphnia* m^{-3} , as in 1999–2000, both types of whitefish never had enough time to consume a full daily ration during day time. This «bottom-up effect» explains starvation leading to markedly reduced growth (Fig. 2).

The summed daily *Daphnia* consumption by whitefish, according to our model estimations (after correction, see above) and observed *Daphnia* densi-

ties, amounted to $0.3\text{--}2\% \text{ d}^{-1}$ of the standing crop of adult *Daphnia* in the lake in summer, and to 1 to $>10\% \text{ d}^{-1}$ in winter and spring (Fig. 8). In 1999 and 2000, estimated theoretical *Daphnia* consumption was between 3 and $>10\% \text{ d}^{-1}$ of the daphnid population during 17 consecutive months.

Daphnia consumption by the whitefish population is positively correlated with *Daphnia* standing crop (Fig. 9). Regression analysis with log-log transformed data results in a significant positive slope ($t = 5.728$, $p < 0.001$). Therefore it can be concluded that the food chain is «bottom-up» controlled, and that the *Daphnia* population is not controlled by whitefish foraging (no «top-down effect»).

Detailed stomach analysis of fish caught in 2001 and 2002 (Maurer and Guthruff, 2005) further allowed a seasonally differentiated food regime as input into the bioenergetics model for these two years. This revealed that between January and May insects (mainly chironomid larvae and pupae) contributed to as much as 90% of the diet of large type whitefish. In spring and early summer, at low *Daphnia* densities, copepods are consumed as well (Fig. 10). Analysing the influence of whitefish on planktonic populations with this differentiated diet shows that for *Daphnia*, consumption by whitefish (assuming equal diets for small type and large type) never exceeded $1.5\% \text{ d}^{-1}$ of total standing crop in 2001–2002. In months with large *Daphnia* populations, fish consumption was lower than $0.5\% \text{ d}^{-1}$. For *Bythotrephes longimanus*, however, daily

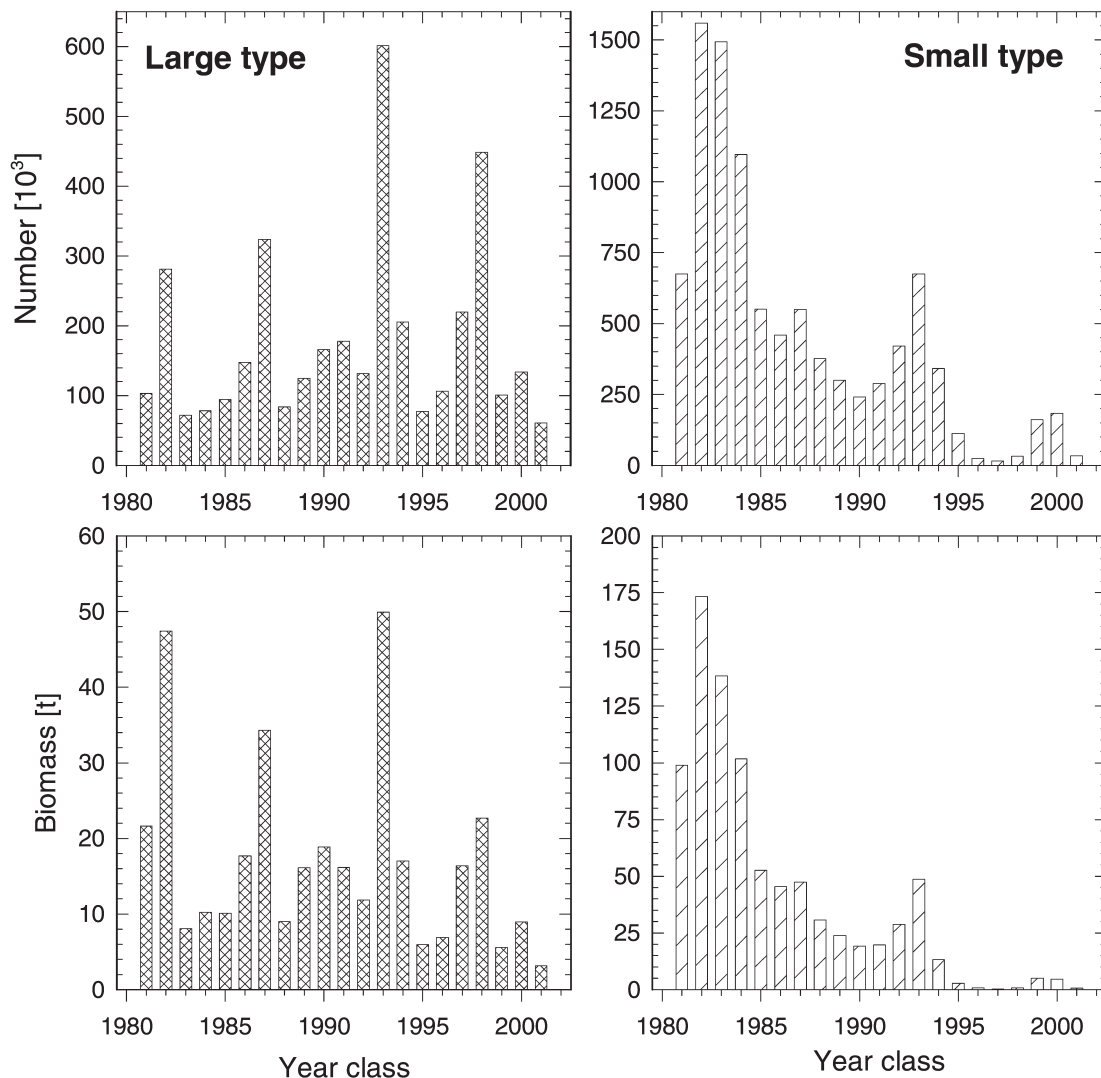


Figure 5. Year class strength (sum of ages 1 to 8) by numbers (top) and weight (bottom) of large type (left) and small type (right) whitefish of Lake Brienz, as computed by virtual population analysis. For details see text.

consumption by all whitefish types could amount to as much as 8 % d⁻¹ of standing crop. For *Leptodora kindtii*, maximum consumption was <5 % d⁻¹.

To study the effect of turbidity on whitefish feeding, two scenarios with extreme light and turbidity conditions in Lake Brienz (data from Jaun et al., 2007) were used to estimate the changes in visual range R and feeding rate f at a constant food density of 100 *Daphnia* m⁻³ at depths from 0 to 80 m (Fig. 11). At low light and low turbidity conditions as on January 18th 2000, visual range R was higher than the feeding range r down to a depth of 51 m, so that feeding rate f was at its maximum value of 0.45 *Daphnia* s⁻¹. It was only below this threshold depth that $R < r$ and thus feeding rate decreased. On August 12, 2003, with high light and high turbidity conditions due to a layer of suspended solids at 14 – 33 m depth, the feeding rate

f was at its maximum down to 13 m depth, then decreased rapidly. The threshold depth for $R = r$ was at 16 m, and at 19 m depth f had already decreased to 10 % of its maximum value, inhibiting feeding of whitefish. Between depths of 35 to 42 m, visibility was higher again, which would theoretically allow some feeding activity, if planktonic organisms were present. However, light intensity at this depth did not allow optical foraging by whitefish. Estimating the threshold depth z_{critical} with $R = r$ as a function of the attenuation coefficient K with low ($E_0 = 500 \mu\text{E m}^{-2} \text{s}^{-1}$) and high ($E_0 = 2500 \mu\text{E m}^{-2} \text{s}^{-1}$) light intensities shows that z_{critical} is greater than 35 – 40 m depth with $K < 0.4 \text{ m}^{-1}$ (= low turbidity), while with $K > 0.8 \text{ m}^{-1}$ (= very high turbidity) z_{critical} is less than 20 m depth.

The visual range model was then applied to observed *Daphnia* densities, turbidity and light inten-

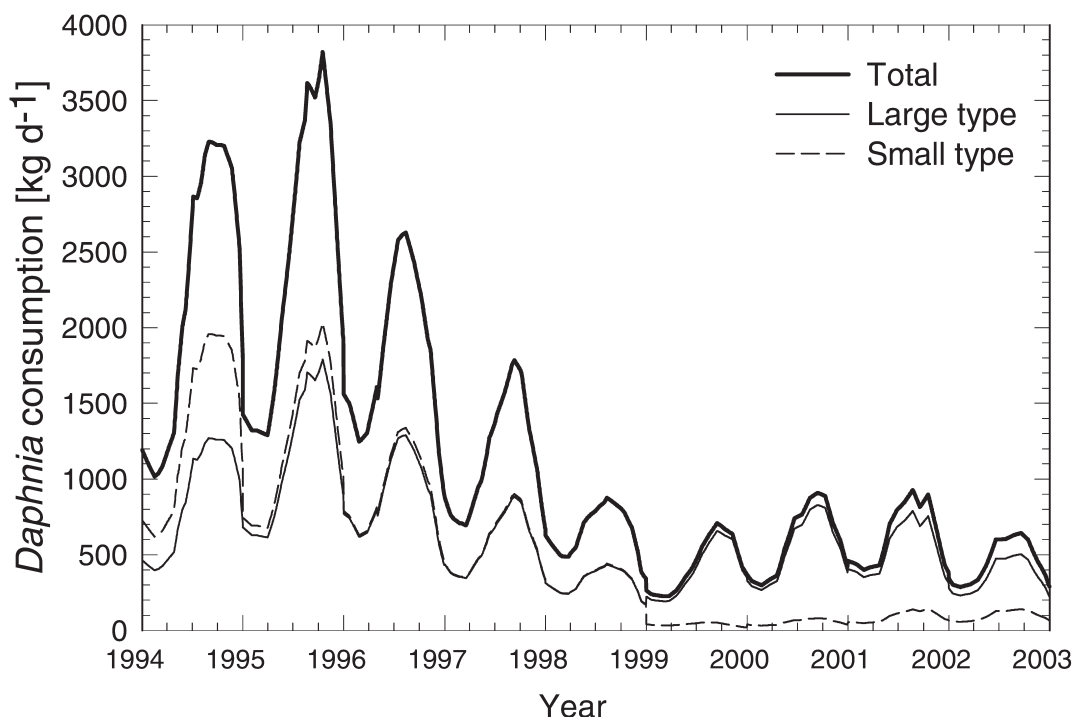


Figure 6. Total consumption of daphnids by small and large type whitefish in Lake Brienz from 1994–2002, based on the bioenergetics model.

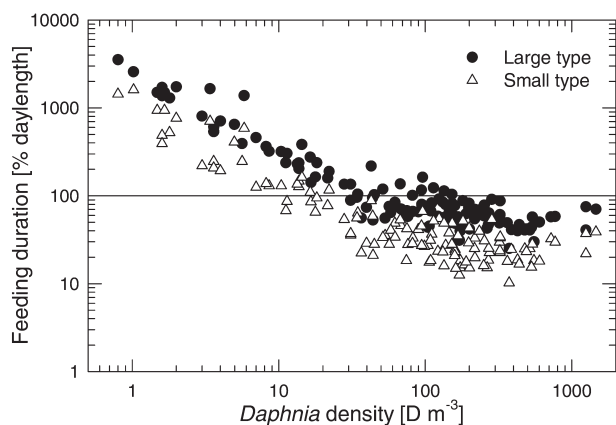


Figure 7. *Daphnia* density and feeding duration of whitefish (= time to consume one daily ration) related to daylength from 1994–2003, resulting from the combination of daily consumption rates according to the bioenergetics model and feeding rates according to the encounter model with observed prey densities. The horizontal line indicates 100%, representing day length of 8 (winter), 12 (spring and autumn) or 16 (summer) hours.

sity data as measured in Lake Brienz 1999–2004 (Jaun et al., 2007). This shows that mean K at noon normally was between 0.16 and 0.65 m^{-1} and only reached higher values of 0.70 in August 2003 and 0.82 m^{-1} in June 2003. Therefore, z_{critical} has been far below a depth of 20 m for most of the time and the feeding rate of whitefish should not have been markedly reduced by insufficient light conditions.

The model then was applied to turbidity and light intensity values resulting from simulations of solids input from dams upstream of the lake (today's situation) and without dams (situation before 1935; Finger et al., 2006). At the euphotic depth z_{eu} (seasonally varying between 6 and 28 m according to measured light data), the feeding rate f varied between $0.25 \text{ Daphnia s}^{-1}$ in winter and $0.9 \text{ Daphnia s}^{-1}$ in summer and autumn while the threshold depth z_{critical} was always below z_{eu} . Today's situation compared to a simulated situation before 1935 shows that without dams, increased concentrations of suspended solids would occur in summer between 10 and 30 m depth. The increase in turbidity compared with today's situation, however, would not be high enough to change visibility within the upper 35 m . It is only below this depth that feeding rate could be restricted by the increase in turbidity without dams.

Discussion

Severe growth retardation and poor condition of the whitefish are the obvious cause for the very low yield of the commercial whitefish fishery in Lake Brienz in 1999 and the first half of 2000. Even though the fish were present in the lake, they could not be caught with the legal gillnet mesh sizes because they were too slim. After growth and condition had resumed in

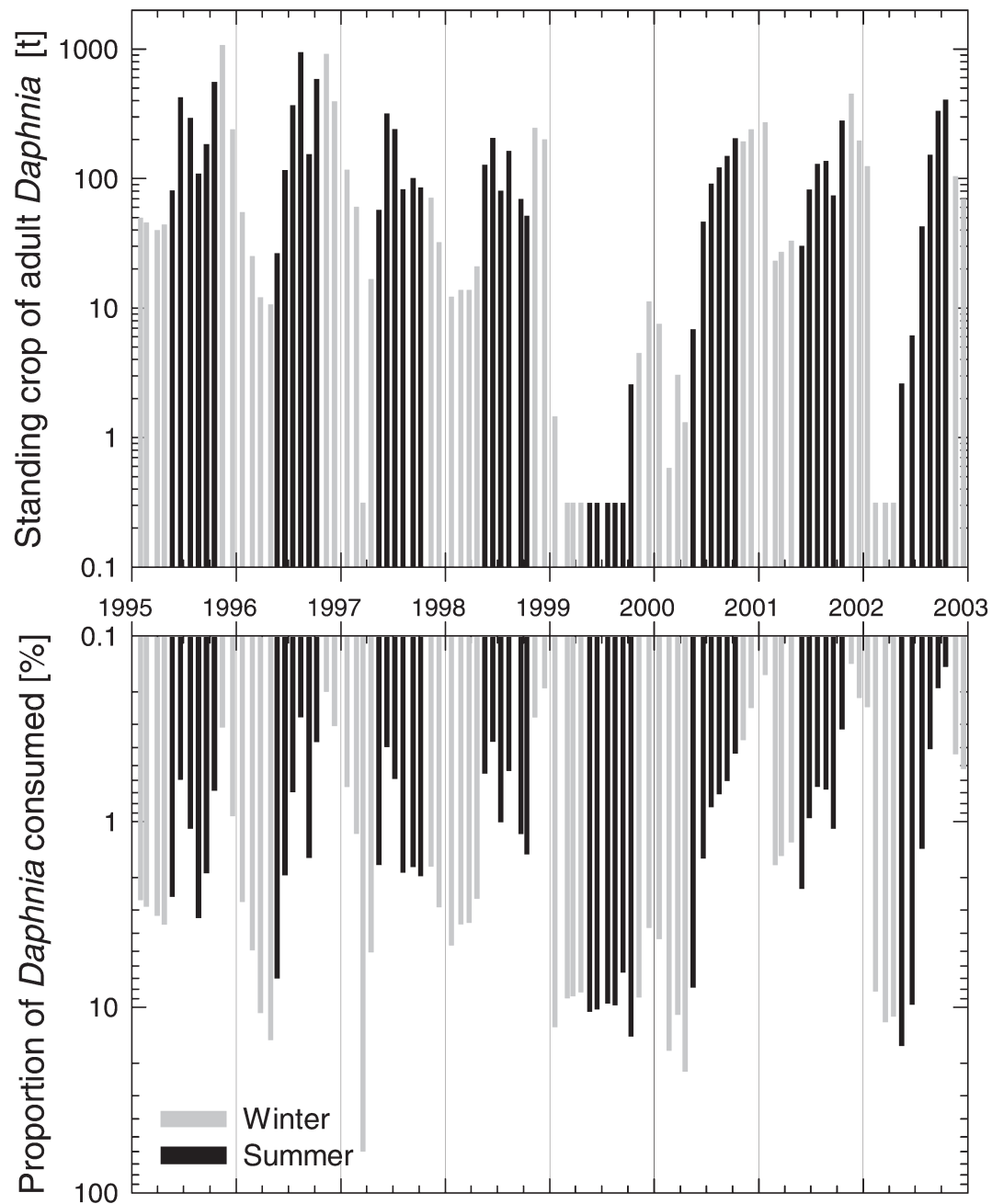


Figure 8. Above: Biomass of adult *Daphnia* as observed in Lake Brienz (0–100 m depth).

Below: theoretical predation on daphnids by whitefish in percent elimination per day for winter (November–April, light) and summer (May–October, dark), as estimated by the application of the bioenergetics model and the encounter model, assuming exclusively adult *Daphnia* as food for whitefish.

the second half of 2000, fishing yield started to increase again.

The marked decrease in growth and condition of the Lake Brienz coregonids during 1999 and until June 2000 coincided with the almost complete absence of cladocerans such as *Daphnia*, *Bythotrephes* and *Lepidodora* from the plankton community. According to stomach analyses from 2001 and 2002, cladocerans are the main food consumed by coregonids of Lake Brienz

(Maurer and Guthruf, 2005). This is clearly the case for the large type coregonid that made up all but two of the 110 stomach samples analysed. While cladocerans were the dominant food category from March – December 2001, benthic chironomid larvae contributed the major part of the food in January, February and April 2002, while copepods were an important food item in March, May and June. Thereafter, cladocerans regained their importance as the domi-

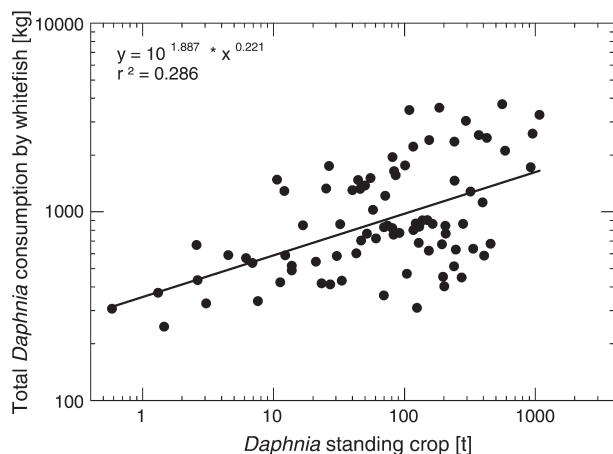


Figure 9. Total estimated *Daphnia* consumption by all whitefish types (monthly means of daily consumption, January 1995 – December 2002) as a function of total *Daphnia* standing crop (monthly samples of years 1995 – 2002) according to the bioenergetics model. *Daphnia* densities below detection level (i.e. 43 *Daphnia* m⁻³, corresponding to a standing crop of 0.314 t for the whole lake) were omitted.

nant food in summer and autumn. The other two stomach samples, belonging to small type whitefish from April and July 2002, contained almost exclusively *Daphnia*, *Bythotrephes* and *Leptodora*, but no benthic food or copepods. These findings are in agreement with the food preference found for coregonids from other central European lakes, where cladocerans are the dominant food source of sub-adult and adult whitefish during the main growing season (Rufli, 1979; Becker and Eckmann, 1992; Mookerji et al., 1998). The observed relationship between daphnid biomass and growth (Fig. 3) points to a more narrow preference for cladocerans in small type whitefish than in large type whitefish that also feed on benthic food and copepods. Also, the early spawning time of small type whitefish (August – September) may have further impeded their growth because these fish suspend feeding during spawning, and their growth is strongly reduced by the lower daphnid abundance in June–July as was observed after 1998 (Rellstab et al., 2007). In contrast, large type whitefish spawn in December. They could therefore benefit from the daphnid peak that still developed in autumn of 2000 and later. Together with their wider food spectrum in winter and spring, this could explain the observed smaller growth decrease of large type whitefish.

Rellstab et al. (2007) provide evidence that *Daphnia* abundance in Lake Brienz is mainly controlled by primary production. They conclude that the decrease in the *Daphnia* population in Lake Brienz in the course of the last 11 years is attributable to decreasing primary production. Our findings also support the existence of a pronounced «bottom-up

effect», not only from primary production to zooplankton, but also from zooplankton to planktivorous fish. To our knowledge, this is the first case where zooplankton abundance, and in particular cladoceran density, has been identified as the key factor in the feeding of whitefish and to their growth and condition. Obviously, the very low abundance of *Daphnia* in 1999 caused the observed growth retardation in both whitefish types, thus making the fish inaccessible to the gillnet fishery. This conclusion is supported by our finding that in these years whitefish simply did not have enough time during the day to consume the number of *Daphnia* necessary to meet the needs for metabolism and growth (Fig. 7). If considering the uncertainties of the two models at the observed very low *Daphnia* densities, this result would persist even if the parameters used for the models should slightly change when adapted to Lake Brienz coregonids. The preference of the two whitefishes for cladocerans during the main growing season in summer and fall must be very strong, otherwise the fish would have switched to feeding on copepods that were always abundant in the lake, even in 1999. Further evidence for the «bottom-up control» of whitefish growth and condition is given by our analysis of *Daphnia* standing crop and consumption, which clearly shows a positive correlation (Fig. 9), indicating that *Daphnia* density controls whitefish consumption. Thus, hypothesis 1, stating that low food (zooplankton) concentration, and in particular the very low abundance of daphnids in 1999–2000, was the driving force behind the decline of the whitefish catch is supported.

As was shown by the bioenergetics model applied to the large and small type coregonid stocks in Lake Brienz, the whitefish seemingly eliminated higher proportions of the cladocerans in 1999 than in earlier years. This result was found in spite of the fact that the biomass of whitefish as determined by VPA had decreased substantially between 1990 and 1999 (Fig. 5). Furthermore, our estimates with the bioenergetics model were based solely on consumption of *Daphnia*, ignoring that large type whitefish – which made up about half of the coregonids in the 1998 and 1999 catch (Table 1) – also feed on benthic food and on copepods at some time of the year (Fig. 10). At the end of 1998, the density of *Daphnia* in the lake representing the start-up population for 1999 was at about the same level as at the end of 1997 (Rellstab et al., 2007). However, contrary to 1998, the *Daphnia* population did not reach detectable levels in 1999. It should be kept in mind that applying the parameters of the «generalized coregonid model» (Rudstam et al., 1994; cited in Hanson et al., 1997) elaborated for North American whitefish to alpine whitefish species for bioenergetic modelling introduces considerable un-

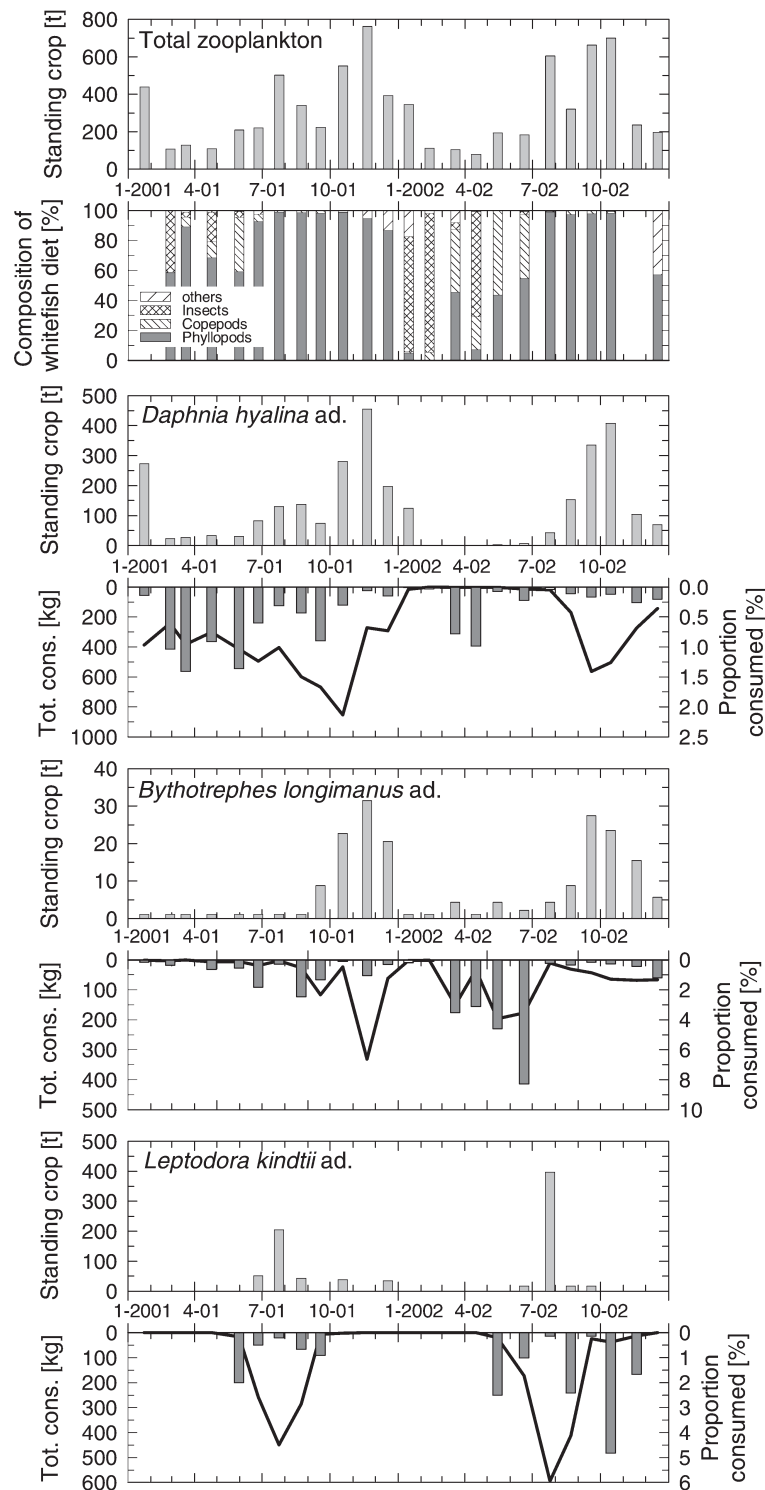


Figure 10. Biomass of total zooplankton in Lake Brienz and diet composition according to stomach samples of large type whitefish in 2001–2002 (top two panels). Standing crop of three main diet zooplankton species (upper bars), total consumption by large type whitefish (lines with left axis), and proportion of prey biomass consumed (lower bars with right axis).

certainty. As pointed out by Madenjian et al. (2006), consumption by whitefish is overestimated when using these model parameters. To account for this we reduced consumption by one third. Without this

reduction, estimated predation rates of whitefish on *Daphnia* would have been higher (0.56 – 4.97% instead of 0.38 – 3.31%) in summers of 1995 – 1997, but still without any detectable effect on the *Daphnia*

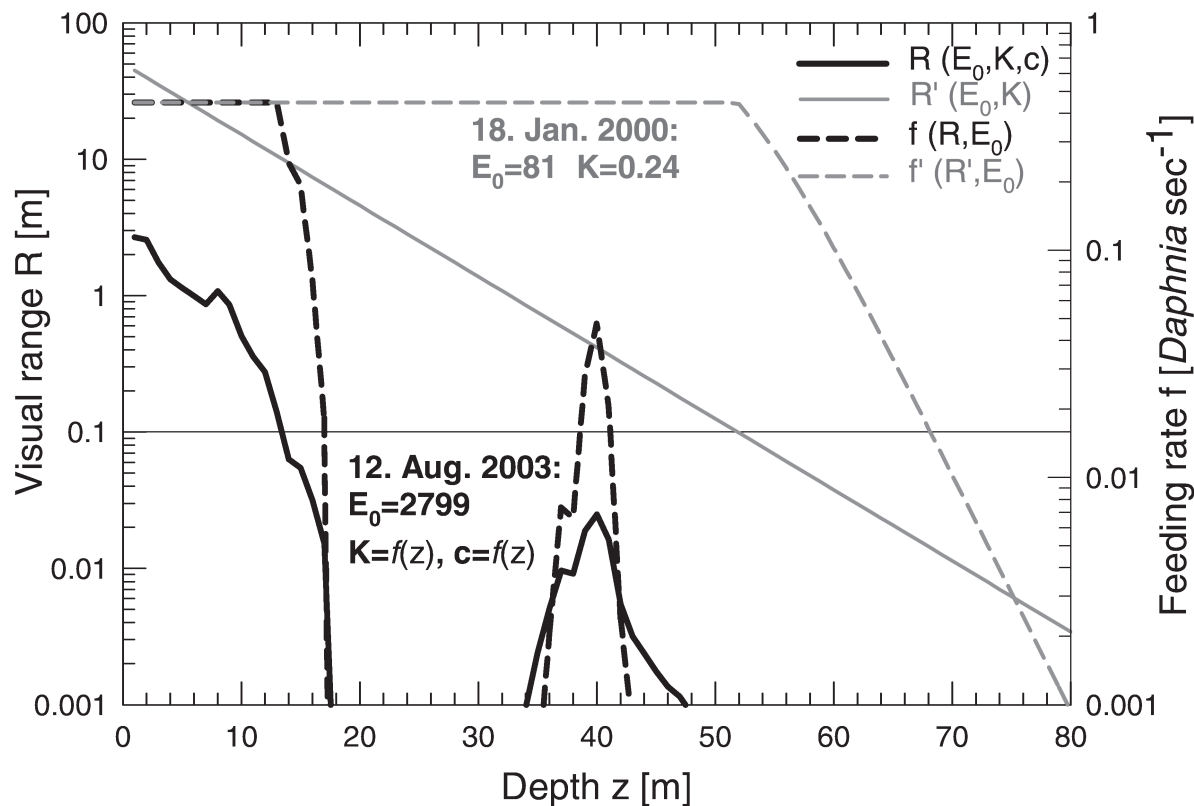


Figure 11. Influence of light intensity and turbidity on visual range R (solid line with left axis) and feeding rate f of whitefish (broken line with right axis) as a function of radiation (E_0), attenuation (K , c) and depth (z) on two days with different light conditions in Lake Brienz. At depth where visual range R equals activity radius $r = 0.1$ m, the feeding rate begins to decline markedly.

population in the following springs. We therefore conclude that in 1999 the Lake Brienz coregonids did not exert such an increased predation pressure as to eliminate almost all *Daphnia* from the lake in a season when phyllopod consumption is at its lowest. Also, during periods of much higher fish biomass in 1995 and 1996, the whitefish never consumed cladocerans so much to make them disappear from plankton samples. We cannot fully exclude that the whitefish in 1999 did not further decimate the already scant *Daphnia* population. Still, the higher *Daphnia* consumption in former and later years does not allow the conclusion that the disappearance of daphnids in 1999 was mainly caused by whitefish predation. This argument is supported by the findings of Rellstab et al. (2007) who conclude that the very low *Daphnia* population in 1999 was primarily the result of low spring water temperature and the extraordinary spring flood in 1999 resulting in a “flushing out effect” of cladocerans. High predation rates on cladocerans always occurred when prey populations were near or even below the detection limit, which introduces further uncertainty into the estimation of predation. However, our results of predation pressure on *Daphnia*, *Bythotrephes* and *Leptodora* by whitefish corre-

spond quite well with model results for Lake Constance zooplankton and whitefish populations (Eckmann et al., 2002). Furthermore, the analysis of the relation between daphnids and whitefish consumption (Fig. 9) clearly indicates a bottom-up control, thus excluding top-down control of foragers over their food organisms. Therefore, hypothesis 2 stating that the daphnid stocks were significantly influenced by whitefish predation between 1995 and 2003 («top-down effect») is rejected.

The encounter and feeding rate models, coupled with information on the effect of reduced visibility on the feeding of fish, did not provide any conclusive evidence that the turbidity occurring in Lake Brienz could have hampered the feeding of whitefish in 1999–2000. The highest turbidity was usually detected at a depth below 10 m (Finger et al., 2006), while the whitefish apparently fed at lesser depths because they were always caught at about 10 m depth or less during the main growing season in summer and autumn (Fisheries Agency of the Canton Bern, unpublished data). Turbidity in 1999 lasted longer but was neither more intensive nor higher up in the depth range of the feeding whitefish than in other years (Finger et al., 2006). Our model estimates show that the feeding rate

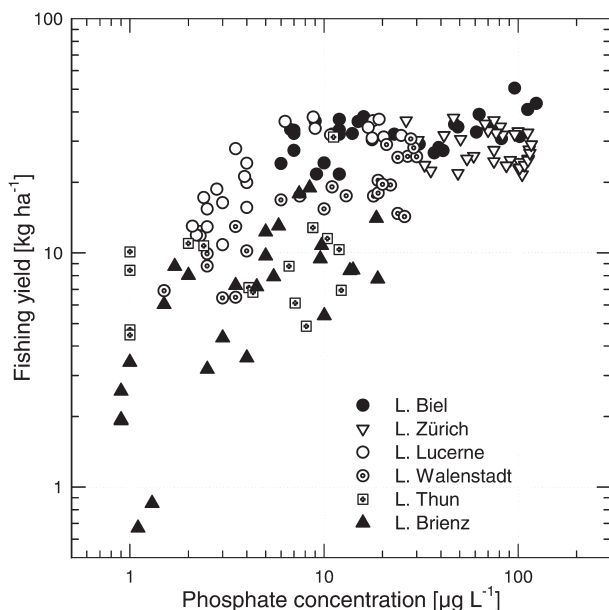


Figure 12. Annual commercial fishing yield, all fish species, in relation to phosphate (soluble reactive phosphorus) concentration during spring circulation in six Swiss lakes with important whitefish stocks.

may be influenced by turbidity below the euphotic depth. However, as minimum light intensity for feeding activity of planktivorous fish (Koski and Johnson, 2002) at noon was at a depth of 9–15 m in summer and at 25–30 m in winter, this does not seem relevant to whitefish in Lake Brienz. Rather, it appears that the density of daphnids and other cladocerans was low already in the beginning of 1999 until June 2000. Hypothesis 3, assuming that elevated turbidity had a strong negative effect on the feeding of the whitefish in 1999 and 2000 is therefore rejected.

Conclusions

Lake Brienz in its present state is a deep, cold and oligotrophic pre-alpine lake with very low primary production. This state is the intended result of the water protection measures taken in fulfilment of the Swiss environmental legislation. Fishing yield is at the end of the production chain and is more or less closely related to primary production. Generally, mesotrophic and moderately eutrophic lakes show high productivity and support high fishing yield, while oligotrophic waters are characterised by low primary production and low fishing yield. It is therefore not surprising that the fishery in Lake Brienz has seen its demise after a number of years with high yields during the mesotrophic period. Our data suggest that this

evolution is primarily the result of the changing nutrient concentration in the lake.

The situation of the Lake Brienz fishery today can be highlighted by comparing its fishing yield and soluble phosphorus (SRP) concentration with that in some other Swiss lakes (Fig. 12). Lake Brienz is clearly situated at the lower end of both phosphorus concentration and yield. Therefore, at a phosphorus concentration around or slightly below $1 \mu\text{g L}^{-1}$, fishing yield in Lake Brienz can be expected to be in the order of about $1\text{--}3 \text{ kg ha}^{-1}$ at best. This includes the yield from the intensified exploitation of the abundant small type whitefish with 20 mm nets legalised in the beginning of 2006.

Comparing the estimated carrying capacity of Lake Brienz with the actual whitefish population as estimated by VPA reveals that the carrying capacity markedly declined from 1995 to 2002 (Fig. 13). During summer and autumn months the whitefish stock was smaller than could be supported by the lake's *Daphnia* production before 1999 and after 2000. However, from January 1999 to May 2000, the whitefish stock clearly exceeded the extraordinarily low carrying capacity as is shown by both models. This finding confirms the above conclusion that the fish were starving in 1999 and 2000. It further supports the above thesis that fishing yield will stay low as long as nutrient concentration and thus the production of whitefish food remain at the present low level. The option of moderately increasing nutrient concentrations by adding phosphorus in a controlled way and thus increasing primary and secondary production and fishing yield (Mills and Chalanchuk, 1988; Mills et al., 1998) is not feasible under the present legal regulations.

Food chains in such oligotrophic systems are fragile, as it has been demonstrated by the 1999 event. Our data document the first case where whitefish populations in ultra-oligotrophic lakes are governed by «bottom-up» control. It is therefore likely that poor cladoceran development and poor growth of whitefish in this system will happen again in the future. Such events are basically beyond human control and go along with ultra-oligotrophic lacustrine systems.

Acknowledgments

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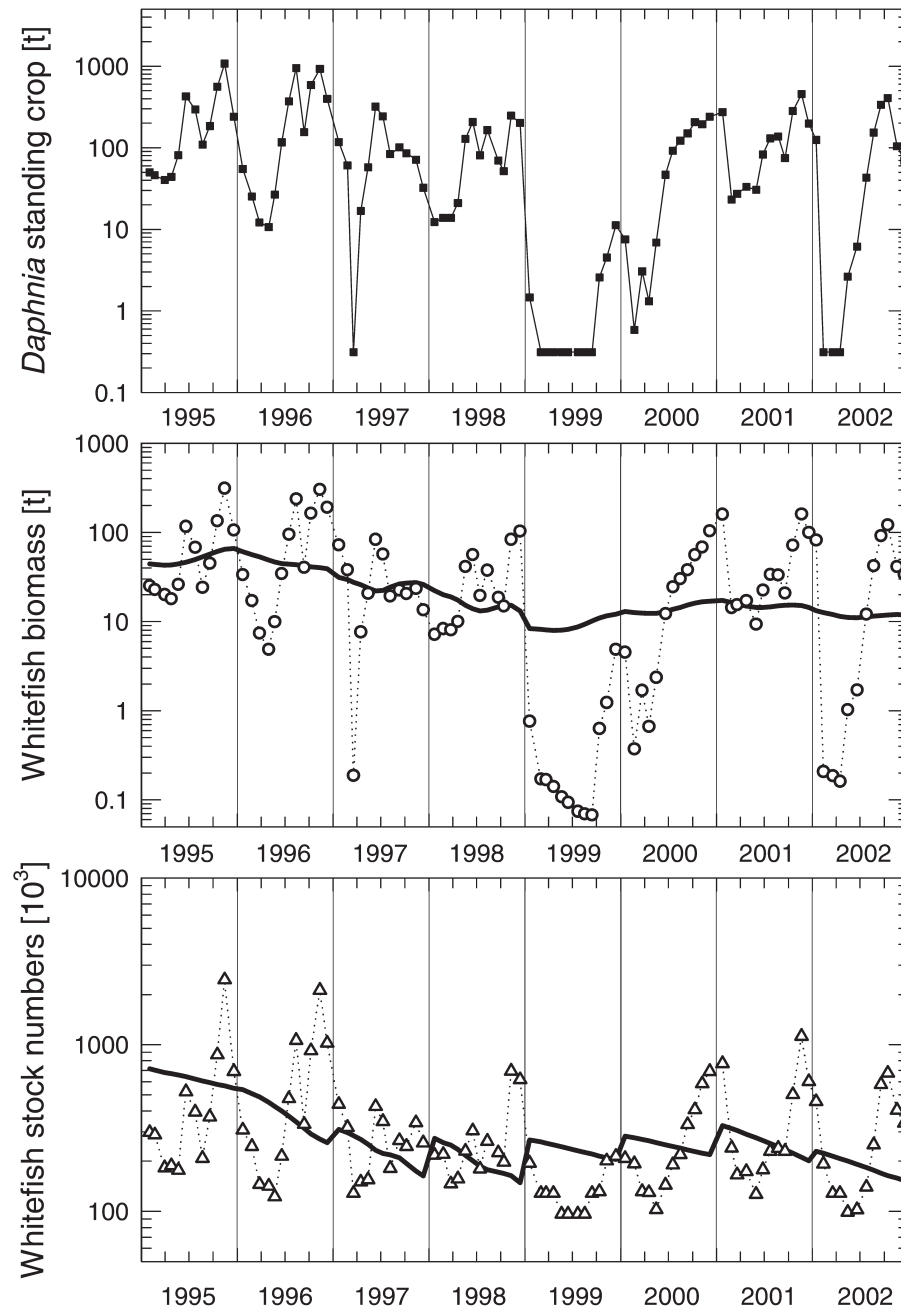


Figure 13. Total *Daphnia* biomass (upper panel), whitefish stock biomass according to VPA (solid line, middle panel) and carrying capacity estimated with the bioenergetics model based on *Daphnia* biomass (open circles, middle panel), whitefish stock in numbers according to VPA (solid line, lower panel) and carrying capacity estimated with the encounter model based on *Daphnia* numbers (open triangles, lower panel).

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